

Body size, reproductive behaviour, and microhabitat use of two sympatric *Trithemis* species – what might allow their sympatry? (Odonata: Libellulidae)

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Abstract. Sympatric territorial species are subject to interference competition when they share the same resources. The interaction becomes stronger when the coexisting species share similar traits, which is often the case in congeners. In this study, we investigated the body size, reproductive behaviour, and microhabitat use of two congeneric dragonflies, *Trithemis annulata* and *T. arteriosa*, in Northeast Algeria from September to November 2012 in order to assess the potential factors that allow their coexistence in the same system. Even though *T. annulata* was larger than *T. arteriosa*, mistaken recognition was often observed. The behavioural sequence of both species exhibited broadly similar patterns in reproductive behaviour but they differed in mate guarding tactics and male-male interference. Copulation duration was shorter in *T. annulata* than in *T. arteriosa*. Oviposition bouts lasted longer in *T. arteriosa* but dipping was faster in *T. annulata*. Analysis of microhabitat choice showed

that *T. arteriosa* males preferred vegetated areas to establish their territories while *T. annulata* used a wide array of habitats including terrestrial ones. Our data suggest that, although the two congeneric species are phenotypically similar and demonstrate low interspecific recognition abilities, they can coexist syntopically because they differ slightly in their habitat use and reproductive behaviour.

Further key words: Dragonfly, interspecific competition, copulation, mate guarding, habitat selection.

Introduction

Understanding the coexistence of species is a major challenge in community ecology. When species share the same habitat at the same time, they are usually likely to interact and compete for valuable resources, such as food or space. Coexistence is even more complex when the species are phenotypically and behaviourally similar (CHESSON 2000), an ecological scenario that happens often between congeneric species. In such cases, some species may use different microhabitats to reduce niche overlap (REHFELDT & HADRYIS 1988; KHELIFA et al. 2013). Therefore, in order to understand the coexistence of closely related species, biological, ecological, and behavioural components have to be taken into account. In the Odonata, territoriality is a common mating parameter in which adult males guard a specific area in the wetlands and defend their territories against conspecifics (SUHONEN et al. 2008). In fact, 'good territories' are subject to huge interference competition because they often offer higher mating success for males by attracting more females (IRUSTA & ARAÚJO 2007). Knowing that individual recognition is based mainly on visual cues and that most congeneric species have similar size, flight, and coloration patterns, interspecific interference competition is common among congeneric males (e.g., TYNKKYNEN et al. 2004, 2005; KHELIFA et al. 2013). In this study, we looked at the coexistence of two congeneric species of *Trithemis* that usually occupy the same aquatic system and have an overlapping reproductive season.

Trithemis annulata (Palisot de Beauvois, 1807) is a medium-sized libellulid, widespread in Africa, Arabia, and the Mediterranean (BOUDOT et al. 2013). In recent decades, it has rapidly expanded its range and has successfully colonized most of Southern Europe (BOUDOT & KALKMAN 2015). *Trithemis arteriosa* (Burmeister, 1839) is a relatively small-sized dragonfly that has a broadly similar distribution as *T. annulata* but it is

still found only locally outside continental Africa (BOUDOT & KALKMAN 2015).

In the present paper, we compare the body size, reproductive behaviour, and microhabitat use of *T. annulata* and *T. arteriosa* during their reproductive season in northeastern Algeria to understand which factors potentially reduce their interaction.

Material and methods

Study site

The study site comprised two artificial ponds of about 0.4 ha at 3 km northwest of El Fedjoudj, Guelma province, Algeria (36°31'54.30"N, 7°22'48.08"E) that were investigated from 25-ix- to 16-xi-2012. The main physical difference between the ponds was the presence of bank vegetation in pond 1 (vegetated pond) and its absence in pond 2 (open pond). Dominant plant species on the bank were *Typha angustifolia*, *Scirpus lacustris*, *Cyperus longus*, and *Paspallum distichum*. Besides *Trithemis annulata* and *T. arteriosa*, the indigenous local dragonfly assemblage comprised *Anax imperator* Leach, 1815, *A. parthenope* Selys, 1839, *Crocothemis erythraea* (Brullé, 1832), *Orthetrum cancellatum* (Linnaeus, 1758), and *Sympetrum fonscolombii* (Selys, 1840). As the study site was investigated from 03-iii- to 16-xi-2012 for other studies, the entire phenology of adults of both species was determined.

Reproductive behaviour survey

This survey was conducted between 28-ix- and 30-x-2012. Daily observations were carried out from about 09:00 h (WAT; UTC +1, solar time), when no individual had arrived yet, to 16:30 h, when all individuals had left the pond. Individuals were captured with a hand net and marked with permanent markers with different combinations of colour spots. Both body and left wing length were measured to the nearest mm with digital callipers. In each pond, two observers surveyed the reproductive behaviour. The duration of copulation, resting, and oviposition was measured, and mate guarding during oviposition was noted.

In order to determine the intensity of intra- and interspecific agonistic interaction, ten mature males of each species were surveyed in their territories during 07–10-ix-2012. When a male flew towards an intruder (male or fe-

male), we considered that a behavioural reaction. The number of reactions, i.e., the chasing towards conspecific or congeneric males and females, was recorded to determine the intensity of male-male competition and interspecific recognition.

Microhabitat choice

Territories that were held by males of both species were recorded during the entire study period. We measured four physical factors in each territory, i.e., bank vegetation height, bank vegetation density within 1 m² and 5 m², distance from land to the shoreline, and submerged plant density. The height at which males perched was estimated visually. The estimation was quite accurate (to the nearest cm) since gridded sticks were placed next to territories. Distances from the shoreline to the oviposition sites where a female dipped her abdomen were estimated to the nearest 5 cm.

Statistical analyses

We used the software R 3.1.2 (R DEVELOPMENT CORE TEAM 2015) to analyse data. Residuals were first checked for normality. Mann-Whitney U tests were used to look for potential differences in size between species and sexes, in vertical and horizontal distribution of males between species, in copulation, oviposition, and abdomen dipping rate between species. Chi-square tests were used to check for significant interspecific interaction between male-male and male-female of both species. A PCA was carried out with the package 'vegan' (OKSANEN et al. 2013) based on four environmental factors taken from the territories to determine differences in habitat preferences between the two species. Values presented hereafter are mean \pm SD.

Results

Adult phenology

At the study sites, reproductively active adults of *Trithemis annulata* started to appear at the water in late May while *T. artemesia* began reproducing in early June. The reproduction period of both species peaked in late July and August. In September the number of individuals decreased gradually and in late October considerably. The end of the flight season was recorded in mid-November.

Body size

In males, body length was significantly larger in *T. annulata* (36.15 ± 1.68 mm, $n = 98$) than in *T. arteriosa* (31.87 ± 1.05 mm, $n = 60$) ($W = 5816$, $p < 0.0001$). Similarly, body length was significantly larger in female *T. annulata* (34.00 ± 1.48 mm, $n = 59$) than in female *T. arteriosa* (30.86 ± 1.65 mm, $n = 40$) ($W = 2201$, $p < 0.0001$). Wing length was also greater in *T. annulata* in both males (27.37 ± 1.37 mm, $n = 98$, vs 23.67 ± 0.68 mm, $n = 60$; $W = 5871$, $p < 0.0001$) and females (26.82 ± 1.48 mm, $n = 59$, vs 23.95 ± 1.65 mm, $n = 40$; $W = 2293$, $p < 0.0001$).

Body length showed SSD in both species ($W = 943$, $p < 0.0001$, $W = 607.5$, $p < 0.0001$ in *T. annulata* and *T. arteriosa*, respectively; Fig. 1a). However, wing length displayed significant SSD only in *T. annulata* ($W = 2208.5$, $p = 0.01$) but not in *T. arteriosa* ($W = 1410.5$, $p = 0.13$; Fig. 1b).

Microhabitat choice

Trithemis arteriosa was restricted to the vegetated pond and was never observed at the open pond while, on the other hand, *T. annulata* frequented both ponds. Table 1 presents the eigenvalues, eigenvectors, and percentage of variance explained by the two first principal components. The two principal components that we retained explained 84.5 % of the total variance. PC1 and PC2 described 60.5 % and 24.0 % of the cumulative variance, respective-

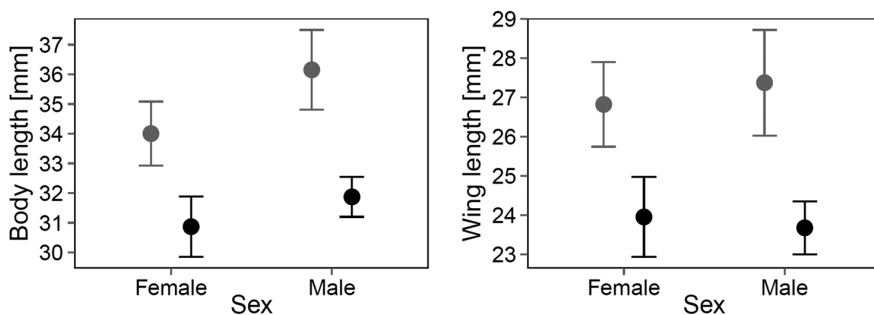


Figure 1. Body and wing length of *Trithemis annulata* and *T. arteriosa* of both males and females, measured at the study site near El Fedjoudj, Guelma province, Algeria, from 28-ix- to 30-x-2012. Black and grey error bars refer to *T. arteriosa* and *T. annulata*, respectively. Error bars are 95 % confidence intervals.

Table 1. Eigenvalues, percentage of variance explained, and eigenvectors of the principal component analysis of microhabitat choice of *Trithemis annulata* and *T. arteriosa* at the study site near El Fedjoudj, Guelma province, Algeria, from 25-ix- to 16-xi-2012. Eigenvectors larger than 0.40 (absolute value) are printed in bold type.

	PC1	PC2
Eigenvalues	1.556	0.980
Proportion of Variance	0.605	0.240
Cumulative Proportion	0.605	0.845
Vegetation height	-0.58	0.04
Vegetation density within 1 m ²	-0.57	0.04
Vegetation density within 5 m ²	-0.20	-0.95
Distance from the shore	-0.53	0.27

ly. Three variables: vegetation height, vegetation density within 1 m², and distance from the shore were negatively correlated to PC1, whereas only vegetation density within 5 m² was negatively related to PC2. In Figure 2, the biplot which is based on four environmental factors and 30 reproductive territories, reveals that *T. annulata* territories were isolated from those of *T. arteriosa* and that the microhabitat overlap was small.

Physical characteristics of reproductive territories of *T. annulata* and *T. arteriosa* are presented in Table 2: Vegetation height was not significantly different between species. Vegetation density within 1 m² was higher in *T. arteriosa* but vegetation density within 5 m² was higher in *T. annulata*. Distance from the shore was greater in *T. arteriosa* than for *T. annulata* (Table 2).

There was a significant difference in the vertical stratification of the perching sites of reproductive males between the two congeneric species ($W = 39.5, p = 0.01$). *Trithemis arteriosa* used only plant supports and showed a mean perching height of 43.8 ± 13.1 cm ($n = 9$), while *T. annulata* used different supports including plants, stones, and the ground with a mean perching height of 31.6 ± 26.1 cm ($n = 21$). Considering only plant support, both species did not show a significant difference in the vertical stratification of perching sites ($W = 39.5, p = 0.07$).

Table 2. Physical characteristics of reproductive territories of *Trithemis annulata* and *T. arteriosa* at the study site near El Fedjoudj, Guelma province, Algeria, from 25-ix- to 16-xi-2012. Values are mean \pm SD. Vegetation density within 1 m² and 5 m² were arcsin transformed before conducting the Mann-Whitney U test.

	<i>T. annulata</i>	<i>T. arteriosa</i>	Mann-Whitney U (p-value)
Vegetation height [cm]	93.85 \pm 72.66	119.66 \pm 34.28	0.38
Vegetation density within 1 m ² [%]	38.80 \pm 29.53	64.44 \pm 12.10	0.02
Vegetation density within 5 m ² [%]	47.38 \pm 17.29	31.11 \pm 7.81	0.01
Distance from the shore [cm]	-6.66 \pm 20.02	12.22 \pm 16.79	0.02

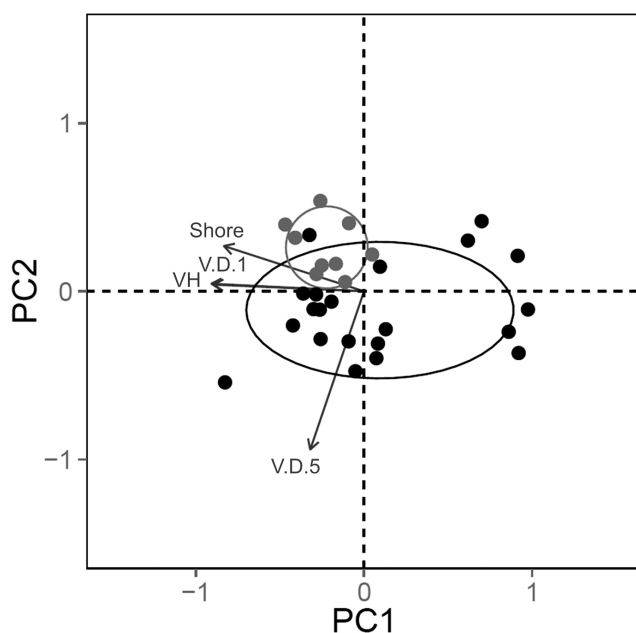


Figure 2. PCA Biplot of microhabitat choice of *Trithemis annulata* and *T. arteriosa* reproductive territories at the study site near El Fedjoudj, Guelma province, Algeria, from 25-ix- to 16-xi-2012. Dark and light grey colours represent *Trithemis annulata* and *T. arteriosa*, respectively. The points represent reproductive territories. Ellipses representing 95 % confidence areas divide territories according to species using Bray-Curtis dissimilarity index. V.D.1 – Vegetation density within 1 m²; V.D.5 – vegetation density within 5 m²; V.H – vegetation height; Shore – distance from the shore.

Table 3. Characteristics of some behavioural parameters (Mean \pm SD, range, and n) of reproduction of *Trithemis annulata* and *T. arteriosa*, recorded at the study site near El Fedjoudj, Guelma province, Algeria, from 25-ix- to 16-xi-2012.

	<i>T. arteriosa</i>	<i>T. annulata</i>	Mann-Whitney U (<i>p</i> -value)
Copulation duration [s]	10.72 \pm 3.41 2–17 23	6.94 \pm 2.72 2.5–14.5 84	<0.0001
Oviposition bout duration [s]	71.08 \pm 12.10 43–88 12	48.52 \pm 16.66 22–81 19	0.0008
Dipping rate [dip/s]	0.79 \pm 0.18 0.51–1.07 12	0.98 \pm 0.28 0.53–1.57 19	0.03
Number of dips	48.02 \pm 20.25 14–72 12	56.25 \pm 14.05 22–72 19	0.14

Reproductive behaviour

Both species demonstrated similar reproductive sequences. The territories were established by males in early morning. Males defended their territories against conspecifics from a perching site. When a female arrived at the water, the male grasped her in flight and copulated most of the time in the air. After copulation, the male directly patrolled the territory and chased other conspecifics while the female rested shortly. The female flew towards the water to oviposit, and at the same time, the male displayed non-contact guarding. The female dipped her abdomen on the water surface close to the shore. After oviposition, the female left the water while the male stayed in the territory. Table 3 presents details about some behavioural components of the reproduction of both species. Copulation duration was significantly longer in *T. arteriosa* than *T. annulata* ($W = 317.5$, $p < 0.0001$). Oviposition bout duration was also longer in *T. arteriosa* ($W = 31$, $p = 0.0008$) but dipping occurred faster in *T. annulata* ($W = 166$, $p = 0.03$). The number of dips was not significantly different between the two species ($W = 78$, $p = 0.14$).

After copulation and in the presence of conspecific harassing males, the male of *T. annulata* guarded his mate very close-by flying rapidly below her abdomen and staying in this position while following the female movements with a perfect synchrony. We refer to this mate guarding behaviour as 'shadow-like non-contact guarding' because in this situation the male follows the female like a shadow (Fig. 3). When the harassment of other males was intense, the reproductive pair synchronously flew vertically very high, up to 20 m, and left the pond to come back later. This guarding behaviour has never been observed in *T. arteriosa*.

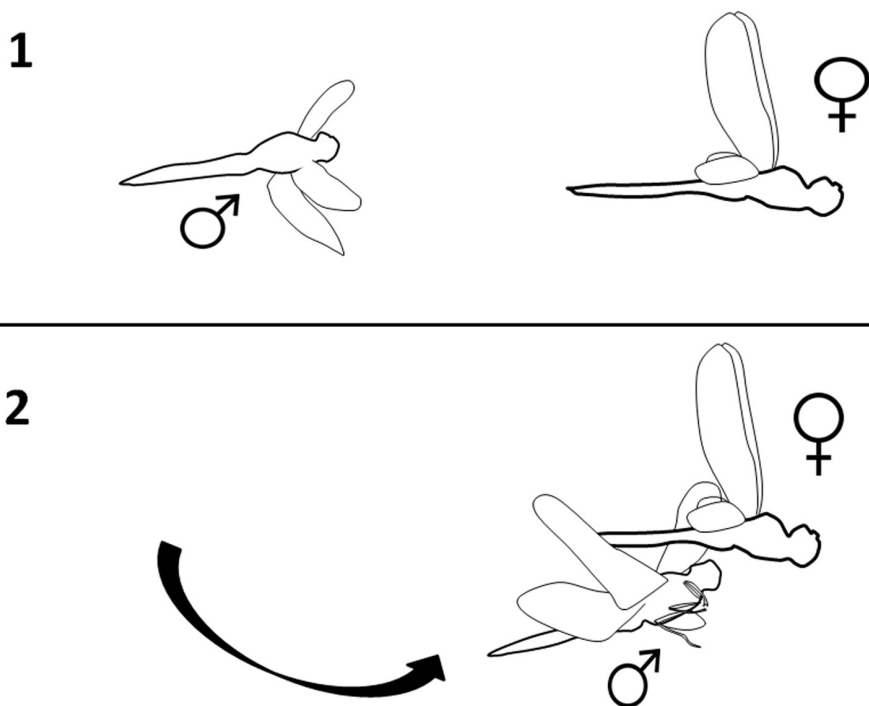


Figure 3. Mate guarding of *Trithemis annulata*. 1 – Non-contact guarding: when there is no interfering male in the oviposition area the reproductive male is not close to the female. 2 – Shadow-like guarding: in the presence of harassing males the reproductive male flies rapidly beneath the female and stays there, simulating the female flight pattern. When the interference stops, the male continues with non-contact guarding.

Trithemis arteriosa males chased conspecific males from their territories in a particular manner. The territorial male headed to the intruder and encircled him repeatedly while the latter hovered on the spot and seemed unable to escape. This behaviour, designated here as 'spinning flight', was observed nine times in eight different males, and it always ended up in the departure of the intruder.

The analysis of interspecific agonistic behaviour showed that *T. annulata* males responded aggressively to *T. arteriosa* males ($\chi^2 = 13.71$, $p = 0.0002$, $n = 42$) and vice versa ($\chi^2 = 7$, $p = 0.008$, $n = 28$). In the same way, *T. annulata* males tried to grasp females of *T. arteriosa* ($\chi^2 = 8.06$, $p = 0.004$, $n = 15$) and vice versa ($\chi^2 = 6.4$, $p = 0.01$, $n = 10$). On one occasion, a *T. annulata* male was observed forming a tandem with a *T. arteriosa* female and trying unsuccessfully to form the copulation wheel.

Discussion

This study showed some morphological, ecological, and behavioural differences between two congeneric species which might explain their simultaneous coexistence in the same habitat. First, there was significant interspecific difference in body size in both males and females. Second, one species was restricted to vegetated sites while the other one used a variety of microhabitats. Finally, even though both species interacted agonistically towards each other during the reproductive season, they showed different behaviour patterns.

Even though *Trithemis annulata* was larger than *T. arteriosa*, both species showed agonistic behaviour towards each other. The slight difference in size and coloration may not suffice for territorial males to distinguish between species (SCHULTZ & SWITZER 2001; SCHULTZ et al. 2008; SINGER 1989). In libellulids, there are other morphological traits than size that males take into account to recognize conspecifics, such as body and wing coloration (PAJUNEN 1964). As demonstrated by FRANTSEVICH & MOKRUSHOV (1984), in males of *Sympetrum danae* (Sulzer, 1776), *S. sanguineum* (O.F. Müller, 1764), and *S. flaveolum* (Linnaeus, 1758), mistaken species recognition often occurs, obviously because species-specific wing patterns are lacking. Similarly, males of four species of *Mnais* are unable to differentiate conspecific females and congeneric hyaline-winged males (SUZUKI & MIYACHI 1996). Therefore, we suggest that in the studied species, which both have

hyaline wings and red-coloured bodies, the slight difference in size is not enough to reduce interference.

The two congeneric species showed different microhabitat use during the reproductive season. Males of *T. arteriosa* chose territories within vegetated areas, similar to what has been briefly described by SUHLING & MARTENS (2007) and WILDERMUTH & MARTENS (2014), while those of *T. annulata* held various territories in both vegetated and open areas. This segregation in habitat use plays an important role in reducing interference between the congeneric males as has been shown in other studies (SCHOENER 1974; ALBRECHT & GOTELLI 2001; HOFER et al. 2004; BUTT & TAHIR 2010). Similar differential microhabitat choice was observed in three congeneric species colonizing streams, viz. *Orthetrum chrysostigma* (Burmeister, 1839), *O. coerulescens* (Fabricius, 1798), and *O. nitidinerve* (Selys, 1841) (KHELIFA et al. 2013). Males of the three species interacted agonistically when they encountered each other. The smallest species (*O. coerulescens*) used mainly highly vegetated areas, the medium-sized species (*O. chrysostigma*) occupied open areas while the largest species (*O. nitidinerve*) had broader habitat choice, including mainly open and also vegetated areas (KHELIFA et al. 2013). In our study, habitat use did not change throughout the season. Even though the adult population size of *T. annulata* decreased at the end of the reproductive season, there was no microhabitat shift in the males of *T. arteriosa*, which suggests that the choice of vegetated areas was not due to competitive exclusion by territorial males of *T. annulata* but rather the result of species specific habitat selection (CORBET 1999).

Copulation duration of *T. annulata* was similar to that reported for *Crocothemis erythraea* (7.0 ± 3.3 s; SIVA-JOTHY 1988), while *T. arteriosa* had a relatively longer copulation duration (10.72 ± 3.41 s), similar to that of *Acisoma panorpoides* Rambur, 1842 (KANO & KITA 1992). In addition, the duration of oviposition bouts was longer in *T. arteriosa* than in *T. annulata* but the dipping rate was higher in *T. annulata*. KOCH & SUHLING (2005) report a lower dipping rate (0.39 ± 0.22 dips/s, $n=23$) in *T. annulata* that was the result of longer oviposition durations (71.25 ± 41.33 s, $n=23$) and lower numbers of dips per bout (23.43 ± 13.54 , $n=23$). Possible factors that might explain this large difference are female size, age, and intra- and interspecific male harassment. The dipping rate and the number of dips of *T. an-*

nulata were similar to that of *T. kirbyi* Selys, 1891 (0.91 ± 0.40 dips/s, $n = 83$; 51.25 ± 41.42 , $n = 84$, respectively); a congeneric species with similar body size. The oviposition duration of *T. arteriosa* found in our study was similar to that of *T. annulata* as determined by KOCH & SUHLING (2005).

To our knowledge, the reproductive behaviour of both congeneric species has not been described in detail so far. Nevertheless, we could list the two species in the category resource-defending polygyny as suggested by EMLEN & ORING (1977) or to the short copulation mating system proposed by CORBET (1999). The shadow-like guarding behaviour of *T. annulata* is unique among North African libellulids, and to our knowledge it has not been described in any species before. The fact that the male covers the underside of the female's abdomen suggests that flying males chase the female from below to proceed to pair formation. Compared to the widespread non-contact guarding in which males defend the female from a certain distance, the shadow-like guarding might be a more effective way to deter copulation with another male. In fact, the non-contact guarding is not efficient when male density is high because, when the reproductive male chases another conspecific, a third male could copulate with the unguarded female (WOLF et al. 1989). Future studies should investigate the evolution of this behaviour and its implication in the overall reproductive success of both males and females. The spinning flight of residential *T. arteriosa* males that end up in the escape of the intruder after having been tightly encircled several times is a special behaviour of this species that has not been reported in the literature yet. Further investigations are required to see whether this behaviour is correlated to body size or other morphological characters and to determine its importance in mating success.

This field study revealed that *T. annulata* and *T. arteriosa* have different sizes, microhabitat use, and reproductive behaviour. These morphological, ecological and behavioural differences may play an important role in reducing the interspecific competition between those closely related species. Further studies should investigate the coexistence of the species at the larval stage and seek to understand the ecological levels at which the species are segregated. Furthermore, knowledge of the ecological consequences of the colonization of these two species of new habitats is the key to predict the effects of range extension on local communities.

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References

- ALBRECHT M. & GOTELLI N.J. 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126: 134-141
- BOUDOT J.-P., CLAUSNITZER V., FERREIRA S., SUHLING F., DIJKSTRA K.-D.B., SCHNEIDER W. & SAMRAOUI B. 2013. *Trithemis annulata*. In: The IUCN Red List of threatened species 2013. Online on the internet, URL [15-iv-2016]: <http://www.iucnredlist.org/details/60052/0>
- BOUDOT J.-P. & KALKMAN V.J. 2015. Atlas of the European dragonflies and damselflies. KNNV Uitgeverij, Utrecht
- BUTT A. & TAHIR H.M. 2010. Resource partitioning among five agrobiont spiders of a rice ecosystem. *Zoological Studies* 49: 470-480
- CHESSON P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*: 343-366
- CORBET P.S. 1999. Dragonflies: behaviour and ecology of Odonata. Harley Books, Colchester
- EMLEN S.T. & ORING L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223
- FRANTSEVICH L. & MOKRUSHOV P. 1984. Visual stimuli releasing attack of a territorial male in *Sympetrum* (Anisoptera: Libellulidae). *Odonatologica* 13: 335-350
- HOFER U., BERSIER L.-F. & BORCARD D. 2004. Relating niche and spatial overlap at the community level. *Oikos* 106: 366-376
- IRUSTA J.B. & ARAÚJO A. 2007. Reproductive tactics of sexes and fitness in the dragonfly, *Diastatops obscura*. *Journal of Insect Science* 7: 24
- KANO K. & KITA H. 1992. Observation of multiple copulations of *Acisoma panorpoides panorpoides* and its breeding. *Gekkan-Mushi* 286: 7-8
- KHELIFA R., ZEBBA R., MOUSSAOUI A., KHALERRAS A., BENSOUILAH S. & MAHDJOUH H. 2013. Niche partitioning in three sympatric congeneric species of dragonfly, *Orthetrum chrysostigma*, *O. coerulescens anceps*, and *O. nitidinerve*: The importance of microhabitat. *Journal of Insect Science* 13: 71
- KOCH K. & SUHLING F. 2005. Do behavioural and life-history traits vary with mate-guarding intensity in libellulid odonates? *Canadian Journal of Zoology* 83: 1631-1637
- OKSANEN J., BLANCHET F.G., KINDT R., LEGENDRE P., MINCHIN P.R., O'HARA R.B., SIMPSON G.L., SOLYMOS P., HENRY M., STEVENS H. & WAGNER H. 2013. Vegan community ecology package. Online on the internet, URL [08-iv-2016]: <http://CRAN.R-project.org/package=vegan>

- PAJUNEN V.I. 1964. Aggressive behaviour in *Leucorrhinia caudalis* Charp. (Odon., Libellulidae). *Annales zoologici fennici* 1: 357-369
- REHFELDT G. & HADRY S. 1988. Interspecific competition in sympatric *Sympetrum sanguineum* (Müller) and *S. flaveolum* (L.) (Anisoptera: Libellulidae). *Odonatologica* 17: 213-225
- SCHOENER T.W. 1974. Resource partitioning in ecological communities. *Science* 185: 27-39
- SCHULTZ J.K. & SWITZER P.V. 2001. Pursuit of heterospecific targets by territorial amberwing dragonflies (*Perithemis tenera* Say): a case of mistaken identity. *Journal of Insect Behavior* 14: 607-620
- SCHULTZ T.D., ANDERSON C.N. & SYMES L.B. 2008. The conspicuousness of colour cues in male pond damselflies depends on ambient light and visual system. *Animal Behaviour* 76: 1357-1364
- SINGER F. 1989. Interspecific aggression in *Leucorrhinia* dragonflies: a frequency-dependent discrimination threshold hypothesis. *Behavioral Ecology and Sociobiology* 25: 421-427
- SIVA-JOTHY M. 1988. Sperm "repositioning" in *Crocothemis erythraea*, a libellulid dragonfly with a brief copulation. *Journal of Insect Behavior* 1: 235-245
- SUHLING F. & MARTENS A. 2007. Dragonflies and damselflies of Namibia. Gamsberg Macmillan, Windhoek
- SUHONEN J., RANTALA M.J. & HONKAVAARA J. 2008. Territoriality in odonates. In: A. Córdoba-Aguilar (Ed.), *Dragonflies and damselflies: model organisms for ecological and evolutionary research*: 203-218. Oxford University Press, Oxford
- SUZUKI K. & MIYACHI K. 1996. The ability of territorial males to recognize females in four Japanese *Mnais* species (Zygoptera, Calopterygidae). *Tombo* 39: 2-12
- R DEVELOPMENT CORE TEAM. 2015. R: A language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna (<http://www.r-project.org/>)
- TYNKKYNNEN K., KOTIAHO J.S., LUOJUMÄKI M. & SUHONEN J. 2005. Interspecific aggression causes negative selection on sexual characters. *Evolution* 59: 1838-1843
- TYNKKYNNEN K., RANTALA M. & SUHONEN J. 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *Journal of evolutionary Biology* 17: 759-767
- WILDERMUTH H. & MARTENS A. 2014. *Taschenlexikon der Libellen Europas*. Quelle & Meyer, Wiebelsheim
- WOLF L., WALTZ E., WAKELEY K. & KLOCKOWSKI D. 1989. Copulation duration and sperm competition in white-faced dragonflies (*Leucorrhinia intacta*; Odonata: Libellulidae). *Behavioral Ecology and Sociobiology* 24: 63-68